

Morphological Variability in *Vipera palaestinae* along an Environmental Gradient

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Abstract The effect of local habitat conditions on organisms, including environmentally-induced morphological changes, constitutes an important aspect of macroecology and evolution. The degree of geographic intraspecific variation in body dimensions, corporeal ratios and scalation pattern among male and female Palestine vipers (*Vipera palaestinae*) in Israel were examined. Univariate and multivariate analyses using 20 variable features relating to metric and meristic characters were applied in order to determine the existence of geographic variability in this species. Univariate analysis revealed that the majority of morphological characters possess relatively minor interregional distinctions, with only a few traits demonstrating significant differences. Discriminant analysis of mixed-gender samples using a combination of variables did not distinguish between geographic groups within each sex. The multifactor approach slightly differentiated between samples when sexes were compared separately, but with much overlap. The continuous sampling method revealed no statistically significant relationship between geographic and metric variables across the distribution range. A weak latitudinal cline was observed in snout-vent length, with both sexes being larger in the south. Noticeable temperature-correlated intraspecific variability was found in both body and tail scale counts but not in head scalation features. Generally, both males and females demonstrate the same phenotype-environment correlation. The spatial variations in external morphology suggest that temperature conditions during early ontogenesis may induce quantitative changes in the scalation pattern of *V. palaestinae*.

Keywords *Vipera palaestinae*, geographic variability, scalation pattern, temperature-dependent trends, Viperidae

1. Introduction

Vipera palaestinae (Werner, 1938) is the most common (Mendelssohn, 1963) species of venomous snake in Israel and is currently considered to be a monotypic species. Within the country this oviparous viper inhabits various zoogeographic regions from the northern Negev in the south up to the northern border, occurring in a wide range of biotopes with the exception of sand dunes. The Palestine viper has a typical Mediterranean pattern of distribution, mainly occupying the more humid northern (the Golan Heights and Galilee) and eastern (the Jordan Valley) areas, while avoiding the sandy and dry southern habitats. It is common in light forests, swamps, rocky

hills, fields, plantations and human settlements of the northern and central parts of Israel. *V. palaestinae* shows great ecological plasticity and is found at different elevations, from about 380 m to about 1,400 m above sea level; in areas with very different climates: from less than 300 mm annual mean precipitation and an annual mean temperature of 22°C, to more than 1,000 mm annual mean precipitation and an annual mean temperature of below 15°C, with an occasional blanket of snow for several days (Bouskila and Amitai, 2001).

Previous studies (Mendelssohn, 1963) have focused mainly on observations of this snake in captivity (reproduction, development and growth). A brief description of its external morphology, behavior, distribution and feeding appears in local field guides (Barash and Hoofien, 1956; Disi *et al.*, 2001). The external morphology and geographic variation in a wide range of characters among many of the Palearctic vipers have been well studied (Forsman, 1991; Zuffi and Bonnet, 1999; Tomović and Džukić, 2003; Brito *et al.*, 2006).

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Recently obtained data (Volynchik, 2011) have revealed new information on the scalation pattern, intraspecific variability and sexual dimorphism of *V. palaestinae* in Israel. However, the geographic variability within this species remains unknown.

Israel can be divided longitudinally into three units: the coastal plain, the central mountain range, and the Jordan Rift Valley, which differ from one another in their tectonic structure, topographical elevation, lithology and climate (Klein, 1988). The coastal plain runs parallel to the Mediterranean Sea, with an elevation ranging between 0–150 m above sea level and a width ranging from several km in the north to tens of km in the south. It is characterized by low seasonal/diurnal temperature variations, with average summer temperatures (August) ranging between 23.7–30.2°C, with occasional extremes ranging between 20–34.4°C (at 32°03' N, 34°45' E, 5 m above sea level).

The Galilee (the northern part of the mountain range) and the elevated volcanic plateau of the Golan Heights comprise the mountainous northern regions, ranging from 300 m in the south to 1,200 m above sea level in the north (> 2000 on Mt. Hermon), descending in the direction of the Jordan Rift Valley and the Sea of Galilee. These elevated areas experience a noticeable temperature gradient: average minimum-maximum temperatures for the warmest month (August) are 18.8–29.8°C (average data for the years 1981–2000; Israel Meteorological Service, <http://www.ims.gov.il>), while the extreme (min-max) August temperatures are 14–38.7°C (observed at 32°58' N, 35°30' E, 934 m above sea level).

The Jordan Valley is an elongated depression located along the Israel-Jordan border that includes the Jordan River and the Sea of Galilee, with elevation ranging from 70 m to over 400 m below sea level in the south. The average temperatures in August are high (23.3–37.6°C) and can reach an extreme maximum of 46°C (at the site 32°42' N, 35°34' E, 200 m below sea level). Thus, these three units markedly differ in ecological conditions; their temperature regimes are highly variable and determined by elevation, latitude and proximity to the Mediterranean Sea, which has a moderating effect on the adjacent coastal areas. Moreover, different areas possess different soil-vegetation complexes (Survey Department, 1956) and specific communities of small vertebrates/mammals (Mendelssohn and Yom-Tov, 1999). A morphological comparison of snake groups located in such heterogeneous environments is thus of particular interest.

Many studies have suggested that environmental

conditions during early ontogenesis in reptiles play an important role in determining offspring phenotypes, such as body dimensions, scalation pattern, and locomotor performance, and may also play an important role in their population ecology (Shine *et al.*, 1997; Deeming, 2004). The impact of temperature fluctuations on neonate morphology is likely to be greater in oviparous reptiles such as *V. palaestinae*, which generally cannot control the thermal conditions of their embryos (Lourdais *et al.*, 2004). Embryos of viviparous species, on the other hand, enjoy the buffering effects of the behavioral thermoregulation provided by the mother. Long-term captive observations (Mendelssohn, 1963) have revealed that oviposition in the Palestine viper takes place during the warmest month (August) in Israel. It is therefore logical to assume that the greatest risk of exposure to highest temperature, and its consequences for offspring development, is during this month. I therefore set out to examine the significance of the relationship between the external morphology of the studied specimens and the thermal regime during their incubation period at the sites where they were collected. I also looked for the appearance of latitudinal clines in snout-vent length at the intraspecific level. It is known that one of the most debated ecomorphological questions is that of the application of Bergmann's rule (Bergmann, 1847) to ectothermic animals (Pincheira-Donoso *et al.*, 2008). The rule suggests that body size is positively correlated with latitude and elevation, i. e., with decreasing ambient temperatures. Recent ecological studies have noted that most tetrapods show certain size-latitude trends. Latitudinal clines in body dimensions have been well documented among many species of mammals, birds, reptiles and amphibians (Ashton *et al.*, 2000; Meiri and Dayan, 2003; Ashton, 2004). Nevertheless, the appearance of geographic gradients in body size for ectotherms, including squamates, is still controversial (Pincheira-Donoso *et al.*, 2008; Meiri, 2011).

The main aim of the present study was to analyze the functional connection between ecological conditions and phenotypic variability, and to assess the degree of morphological distinction at the inter-population level. The large sample sizes from the studied regions facilitated the provision of data on the geographic variability of this species. The following questions were asked: Does the *V. palaestinae* population in Israel show geographic morphological variation? Is there a relationship between external characters and latitude, elevation or ambient temperature? What are the possible driving factors in regard to the appearance and development of phenotypic plasticity among these vipers? And, finally, how might

environmental conditions or potential food resources influence the spatial variations in corporeal proportions and scalation pattern?

2. Materials and Methods

I collected data from 290 (167 males and 123 females) preserved specimens of *V. palaestinae* from the Natural History Museum of the Department of Zoology, Faculty of Life Sciences, Tel Aviv University. The specimens had been collected between 1949–2010. To test for inter-regional differences I selected 241 adult vipers and grouped them according to the following areas: “northern” group – snakes from the Golan Heights and Galilee (Golan Heights & Galilee), comprising 40 males and 22 females; “eastern” group – the Jordan Valley (Jordan Valley), 43 males and 43 females; “western” group – the central coastal plain (central coastal plain), 33 males and 25 females; and “south-western” group – the southern coastal plain (southern coastal plain), 24 males and 11 females.

Analyses were conducted with data combined for males and females, as well as for each sex separately. All suitable specimens with a total length > 700 mm, which were considered as adults, were included. The topography of the studied areas is shown in Figure 1. For each snake, I recorded collection data (region and locality with geographic coordinates and elevation, and weight), and I sexed the snakes by tail shape (Volynchik, 2011) and hemipenis eversion. I then measured, for all snakes, snout-vent length (SVL) and tail length (Lcd), head length (Lcap: from the tip of the snout to the quadrate-articular joint, along the longitudinal axis), head width (Wcap: across the widest point), interocular distance (IOD: between the outermost points of the supraocular scales); from these, the ratios SVL/Lcd, SVL/Lcap and Lcap/Wcap were calculated. Body weight (M) was measured to the nearest 1 g; SVL and Lcd were determined to the nearest 1 mm using a ruler or tape measure. Head dimensions were taken with a digital caliper to the nearest 0.1 mm. The number of ventral (ventr), subcaudal (Scd), circumorbital scales; on the right (corbs-r), and on the left (corbs-l) sides, supralabial (suprls-r/suprls-l), sublabial scales (subls-r/subls-l) and midbody scale rows (MSR) were recorded. As I could not record every parameter for each specimen due to the bad condition of some specimens, the sample sizes vary for the different parameters (Table 1).

The climate parameters comprised annual mean temperatures and monthly mean temperatures at the

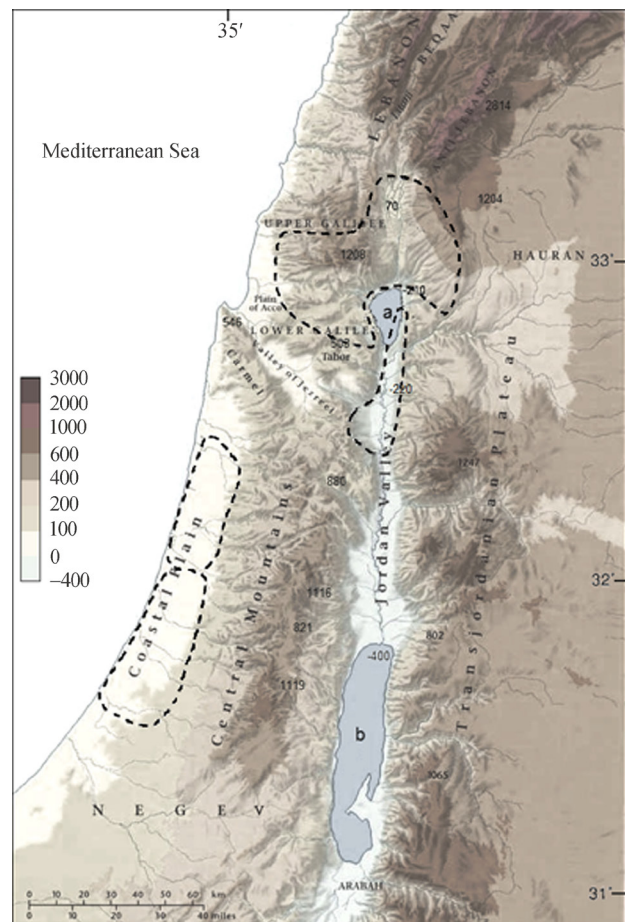


Figure 1 Topographic map of the studied areas.

a: Sea of Galilee; b: Dead Sea. Areas enclosed by dotted line: The studied areas showing Golan Heights & Galilee, Jordan Valley, Central Coastal Plain, and Southern Coastal Plain from north to south.

snakes' natural locations during the incubation period, shortly after oviposition in this species (August). Spatially-interpolated climate data, mainly for the 1950–2000 period, on grids with spatial resolution of 30 arc-second (often referred to as 1-km spatial resolution) were taken from <http://www.worldclim.org> and imported into the GIS application.

I used discriminant function analysis (DFA, standard and forward stepwise methods) to test for the existence of geographic variability in morphology of samples from different zoogeographic areas of Israel, treating region/sex as a grouping variable (in total 8 groups: 4 male and 4 female); one-way ANOVA was used to test for intrasexual comparison in external morphology between localities. I performed post-hoc Tukey's multiple-comparison tests for the parameters that vary geographically in order to determine which samples significantly differed from one another. Analysis of relationships between geographic factors and morphological traits was made by correlation

Table 1 A comparison of morphological features of *Vipera palaestinae* from different zoogeographic areas (one-way ANOVA).

Features		Zoogeographic areas								<i>P</i>	<i>F</i>
		Golan Heights & Galilee		Jordan Valley		Central Coastal Plain		Southern Coastal Plain			
		mean ± SD	n	mean ± SD	n	mean ± SD	n	mean ± SD	n		
M (g)	♂	403.3 ± 139.1	37	376.1 ± 152	43	407.8 ± 166.6	32	513.2 ± 196.8	24	0.01	3.901
	♀	452.6 ± 234.6	21	399.6 ± 167.6	41	501.9 ± 299.9	25	466.8 ± 131.3	11	0.321	1.181
SVL (mm)	♂	860.8 ± 88	40	854 ± 117.3	43	849.2 ± 120.6	33	908.5 ± 121.9	24	0.192	1.597
	♀	852.2 ± 80.4	22	854.5 ± 108.2	43	887.8 ± 100.5	25	909.8 ± 99.5	11	0.243	1.412
Lcd (mm)	♂	120.8 ± 11.5	37	120.7 ± 15.4	43	120 ± 15.7	32	126.5 ± 15.4	24	0.342	1.121
	♀	104.4 ± 9.1	22	104.1 ± 10.3	43	108.8 ± 10.8	25	110.4 ± 9	11	0.12	1.988
Lcap (mm)	♂	41.1 ± 3.3	32	40.5 ± 3.7	33	40.7 ± 4.7	27	42.2 ± 4.7	21	0.532	0.736
	♀	39.9 ± 2.6	19	40 ± 3.2	37	40.7 ± 3.4	24	41.3 ± 3	8	0.603	0.62
Wcap (mm)	♂	28.8 ± 2.5	31	28.5 ± 3.2	30	28.6 ± 3.2	24	29.7 ± 3.9	17	0.665	0.525
	♀	28.5 ± 2.3	18	29.1 ± 3.2	35	30.1 ± 2.7	19	30.3 ± 3	7	0.287	1.279
SVL / Lcd	♂	7.07 ± 0.3	37	7.06 ± 0.3	43	7.06 ± 0.4	32	7.16 ± 0.2	24	0.692	0.486
	♀	8.16 ± 0.4	22	8.18 ± 0.4	43	8.15 ± 0.4	25	8.22 ± 0.4	11	0.971	0.078
SVL / Lcap	♂	21.2 ± 0.7	32	20.6 ± 1.3	33	20.9 ± 0.9	27	21.5 ± 1	21	0.019	3.428
	♀	21 ± 1.1	19	21 ± 1.4	37	21.7 ± 1.3	24	21.6 ± 1.1	8	0.134	1.908
Lcap / Wcap	♂	1.43 ± 0.1	31	1.43 ± 0.1	30	1.41 ± 0	24	1.41 ± 0.1	17	0.78	0.362
	♀	1.39 ± 0.1	18	1.38 ± 0.1	35	1.35 ± 0.1	19	1.37 ± 0.1	7	0.636	0.569
Ventr	♂	164 ± 1.9	40	164.7 ± 2.1	40	164.1 ± 2.1	33	163.5 ± 2.1	24	0.138	1.856
	♀	165.5 ± 2.3	22	166.6 ± 2.2	41	165.9 ± 2.3	25	166.1 ± 2.1	11	0.282	1.29
Scd	♂	40 ± 1.4	38	40.1 ± 1.4	40	40.2 ± 1.5	32	40.1 ± 1.3	24	0.929	0.149
	♀	35.3 ± 1.1	22	35.4 ± 1.1	41	35.8 ± 1.2	25	35.4 ± 1.0	11	0.457	0.873
MSR	♂	25 ± 0.36	37	25 ± 0	39	25.1 ± 0.52	28	24.9 ± 0.41	23	0.113	2.027
	♀	25.2 ± 0.62	21	25.1 ± 0.49	41	25 ± 0	24	25 ± 0	10	0.28	1.297
Corbs-r+l	♂	26.4 ± 1.17	40	26.7 ± 1.26	40	26.4 ± 1.29	32	26.7 ± 1.39	24	0.595	0.632
	♀	25.8 ± 1.09	22	26.3 ± 1.43	40	26.4 ± 1.26	25	26.8 ± 1.32	11	0.18	1.659
Suprls-r+l	♂	20 ± 0	40	19.9 ± 0.54	40	19.9 ± 0.46	33	19.8 ± 0.72	24	0.549	0.707
	♀	20.1 ± 0.68	22	20.2 ± 0.63	40	20 ± 0.61	25	20.4 ± 0.68	11	0.26	1.356
Subls-r+l	♂	24.5 ± 1.03	40	24.5 ± 1.01	40	24.6 ± 1.38	33	24.6 ± 1.04	24	0.94	0.132
	♀	25 ± 1.13	22	24.8 ± 1.19	41	24.8 ± 1.10	25	25.1 ± 1.07	11	0.78	2.701

matrices module. All statistical analyses were done using Statistica 8 (StatSoft, Inc., USA).

3. Results

3.1 Interregional comparison A morphological comparison (one-way ANOVA) between zoogeographic areas using basic metric and meristic features is given in Table 1. On the whole, both sexes displayed similar trends in their corporeal dimensions. Only a few characters showed significant differences between regions (body weight and SVL/Lcap ratio among males). The results of multiple comparison (Tukey's HSD test) for body weight revealed significant differences between the southern coastal plain and the Golan Heights & Galilee groups ($P = 0.045$, $F = 4.17$) and between the southern coastal plain and the Jordan Valley samples ($P = 0.004$, $F = 8.76$); and the SVL/Lcap ratio of the southern coastal plain males significantly differed ($P = 0.015$, $F = 6.21$) from that of the Jordan Valley.

On application of pairwise comparison (one-way ANOVA) when males and females were combined, SVL

of the southern coastal plain group (908.9 ± 113.8 mm, $n = 35$) significantly exceeded that of both the Golan Heights & Galilee (857.8 ± 84.8 mm, $n = 62$; $P = 0.013$, $F = 6.31$) and the Jordan Valley groups (854.2 ± 112.2 mm, $n = 86$; $P = 0.017$, $F = 5.85$), although neither males nor females alone showed significant differences. However, the percentage of large specimens (SVL > 1,000 mm) in the observed groups was unequal. The Golan Heights & Galilee group contained about 6.5% of these snakes (7.5% among males and 4.5% among females), the Jordan Valley group about 11.6% (14% and 9.3%), and the central coastal plain group 15.5% (15% and 16%, respectively). Within the southern coastal plain group this percentage was 34.3% in the mixed-sex sample (37.5% among males and 27.3% among females). Thus, within the range of *V. palaestinae*, the share of large specimens in the samples clearly increases southwards; this tendency was similar for both sexes.

In addition, the data revealed no geographic variation in sexual size dimorphism (SSD), that is, all samples display no significant differences ($P > 0.05$) between sexes in their SVL. Nevertheless, mean adult SVL of

the northern males slightly exceeded that of females; the western group showed an opposite trend; and SVL of both sexes in the eastern and south-western samples was similar (Table 1).

The scalation pattern demonstrated no significant geographic variation, although both males and females from the Jordan Valley had more ventrals, while the central coastal plain vipers had more subcaudals. Other scalation features, such as the number of MSRs, circumorbitals, supra- and sublabials, were less variable in all groups and did not display any noticeable trends.

On application of discriminant function analysis using 20 morphological variables, seven canonical roots were extracted, among which only the first, which describes the intersexual differences, was significant. DFA based on metric and meristic data for both sexes together generated a highly significant discriminant function (root 1; $P < 0.0001$, $\lambda = 0.115$, $\chi^2 = 488.3$), which correctly classified 88.6% of specimens (Table 2). Within this function the basic corporeal dimensions relating to SVL and Lcd (mainly the SVL/Lcd ratio) significantly contributed to discrimination between sexes, thus the first extracted root sharply separated two groups – male and female. Several additional characters contributed to the variance of the

second canonical root ($P = 0.46$, $\lambda = 0.601$, $\chi^2 = 114.8$); in addition to SVL this was mainly head size (Lcap and Wcap), while all other functions together “explain” only a few percent of the variance.

Analysis of relationships among the geographic groups (DFA) revealed the unisexual samples from various areas to be statistically very close, with the squared mahalanobis distances (MD^2) low (0.644–2.987), and no significant differences ($P > 0.05$) in male-male or female-female comparisons. However, males greatly differ from females ($MD^2 = 16.013$ – 20.078), and a comparison between them revealed highly significant ($P < 0.0001$) intersexual distinctions in all cases: the first canonical root, illustrating sexual dimorphism, displays most of the discriminatory power within this mixed-gender sample (Figure 2 A, B); while the second and third roots, displaying intergroup variability, are much less informative and do not distinguish one geographic group from another.

Table 2 Coefficients for canonical variables with successive roots removed (discriminant analysis).

Variables	Standardized coefficients for canonical variables		
	Root 1	Root 2	Root 3
M	0.07746	-0.66886	0.23681
SVL	-1.28830	0.99969	-1.05898
Lcd	0.92833	-0.21623	0.67759
SVL/Lcd	1.41834	-0.52220	0.76064
Lcap	-0.03494	-0.83271	1.30052
Wcap	-0.09148	0.97153	-1.37841
Lcap/Wcap	-0.21433	0.50938	-0.73216
Ventr	0.15257	0.61785	-0.24054
Scd	-0.33471	-0.19282	0.29061
MSR	0.02311	0.10342	0.51363
Suprl-r	0.03793	0.26589	0.28334
Suprl-l	0.01868	0.05677	-0.35896
Sublabl-r	-0.00678	-0.42945	0.25550
Sublabl-l	-0.02222	0.26485	-0.21032
Corbs-r	-0.03136	-0.07258	-0.65699
Corbs-l	-0.00582	0.12008	0.04794
IOD	-0.35903	0.29335	0.21427
SVL/Lcap	-0.12039	-0.73012	-0.27516
SVL/Ventr	-0.96655	0.22470	-1.05649
Lcd/Scd	1.24815	-0.44824	0.54051
Eigenvalue	4.222	0.202	0.156
Cumulative proportion	0.886	0.928	0.961
Wilks'-Lambda	0.115	0.601	0.723
Chi-Sqr.	488.394	114.841	73.199
df	140	114	90
P	<0.0001	0.460	0.901

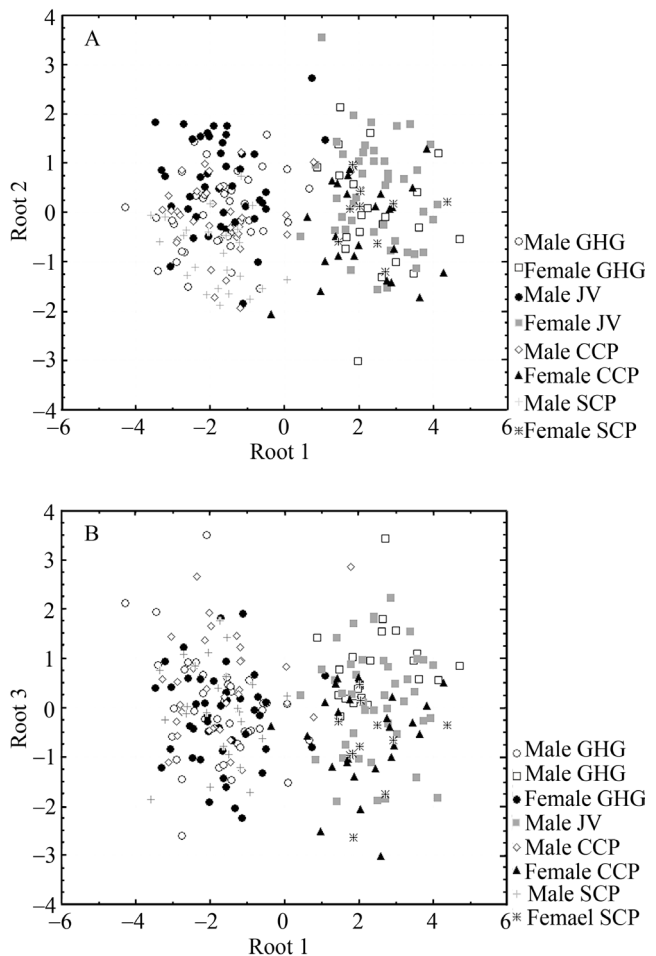


Figure 2 Graphic results of discriminant analysis grouping male and female samples. The relative position of individual specimens in the projection of the first three canonical functions illustrating sexual dimorphism (root 1) and intergroup variability (roots 2, 3). A: Root 1 vs. root 2; B: Root 1 vs. root 3.

DFA (forward stepwise method) using the above morphological variables extracted seven variables in males, in order of significance: SVL/Lcap, M, SVL, subls-r, ventr, MSR, subls-l. The stepwise procedure extracted three canonical roots, the first of which ($P = 0.0009$, $\lambda = 0.702$, $\chi^2 = 47.09$) accounts for 80% of the total intergroup variability. The corporeal measurements (M, SVL) and SVL/Lcap ratio are the most informative for between-group distinction. The second function accounts for 16.2% and the last one for 3.8% of the remaining variability. MSR and subls-r mainly contribute to creation of the second and third canonical roots, respectively.

The analysis for females similarly revealed that the following five variables—corbs-r, SVL/Lcap, MSR, suprls-r and suprls-l—influenced group discrimination. Three canonical roots were extracted, with the first accounting for 76.7% of variances ($P = 0.049$, $\lambda = 0.697$, $\chi^2 = 25.01$). The corbs-r and SVL/Lcap variables showed the strongest contribution to this function, while suprls-r

and MSR mainly contributed to variance of the second and third canonical roots, respectively. Confidence ellipses reflected a large overlap in variation of the canonical functions (Figure 3), and the presence of intraspecific variations without a considerable distinction between geographic groups. Thus, males from the northern sample (Golan Heights & Galilee) are very similar ($MD^2 = 0.116$) morphologically to those of the central coastal plain, whereas the highest degree of dissimilarity was observed between the eastern (Jordan Valley) and the south-western (southern coastal plain) groups ($MD^2 = 2.775$). Among females, the least distances are indicated as being between the Jordan Valley–central coastal plain ($MD^2 = 0.631$) and the Jordan Valley–Golan Heights & Galilee ($MD^2 = 0.656$) samples, while the largest morphological gap ($MD^2 = 3.093$) was recorded between the Golan Heights & Galilee and southern coastal plain groups.

3.2 Environment-related variation Analysis of latitudinal variability in external morphology based on

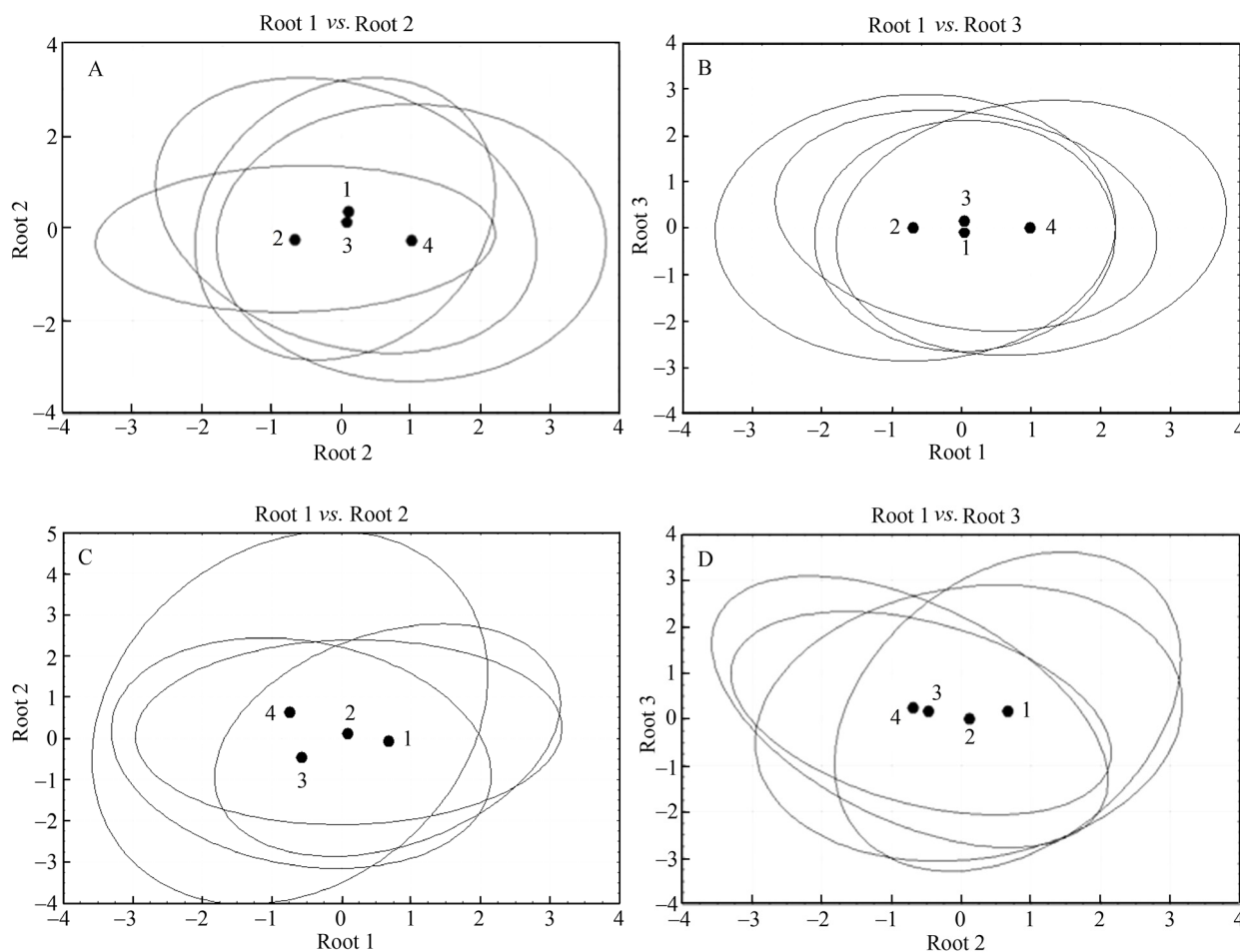


Figure 3 Position of geographic group centroids and confidence ellipses of males (A, B) and females (C, D) in the projection of canonical variates. 1: Golan Heights & Galilee; 2: Jordan Valley; 3: Central Coastal Plain; 4: Southern Coastal Plain; and circles: 95% confidence ellipses.

continuous sampling revealed a negligible relationship between latitude and SVL within the studied areas, with SVL slightly increasing southward ($r = -0.086$, $P = 0.272$, $r^2 = 0.007$ for males; $r = -0.124$, $P = 0.173$, $r^2 = 0.015$ for females). No influence of thermal regime was found (temperatures were uncorrelated with latitude, $r = 0.043$, $P = 0.462$, $r^2 = 0.002$ for annual averages) across the observed areas. Moreover, the local temperature conditions (annual averages) were not found to affect SVL of adults ($r = -0.016$, $P = 0.828$, $r^2 = 0.0003$ for males; $r = -0.044$, $P = 0.625$, $r^2 = 0.002$ for females).

Scalation characters, such as number of ventral and subcaudal scales, also did not display a significant correlation to latitude across the range, although both sexes showed similar temperature-dependent trends. The studied locations are characterized by a highly significant negative correlation between elevation and either annual average ($r = -0.831$, $P < 0.0001$, $r^2 = 0.691$) or August average ($r = -0.680$, $P < 0.0001$, $r^2 = 0.462$) temperatures. Hence, the possible altitude-related morphological variations should be considered as a thermal regime influence. Thus, I observed a marked connection between both body and tail scale counts, and thermal conditions during August (Figure 4 A, B). The number of ventrals in both sexes showed a positive and nearly significant correlation with temperature, in contrast to the number of subcaudals, which revealed the opposite trend—its number was lower at sites with higher temperatures. In the latter case, the recorded correlation between climatic and morphological variables among males was statistically significant, whereas females displayed less noticeable effects. Application of the number of ventrals/number of subcaudals ratio reinforces this finding. The ratio's value significantly increased (Figure 4 C) among specimens inhabiting hot depressions (i. e., the Jordan Valley). However, these body/tail meristic changes did not reflect any corresponding metric modifications; and the relative tail length within the unisexual samples was quite stable ($r = 0.028$, $P = 0.718$, $r^2 = 0.0008$ for males; $r = 0.056$, $P = 0.538$, $r^2 = 0.003$ for females) despite the different thermal influence throughout embryonic growth. It is interesting to note that the other scalation components (number of circumorbital, supralabial and sublabial scales) did not demonstrate any temperature-related variability.

4. Discussion

Geographic variability and its degree have been widely investigated among many reptile species (Thorpe,

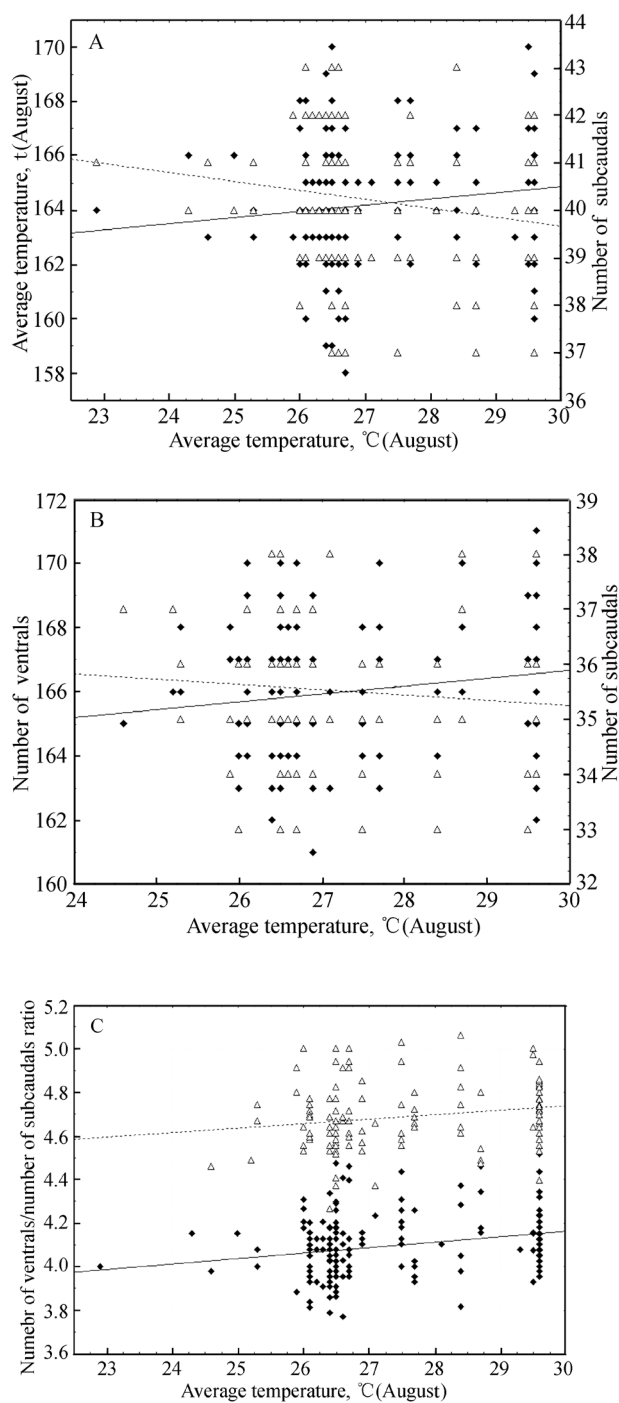


Figure 4 Functional connection between ambient temperature and body/tail-related characters. A, B: Temperature-related variations of body/tail scalation pattern. Males (A); ventrals: $y = 158.05 + 0.22x$; $n = 163$; $r = 0.1524$; $P = 0.0521$; $r^2 = 0.0232$; subcaudals: $y = 45.31 - 0.18x$; $n = 161$; $r = -0.1900$; $P = 0.0158$; $r^2 = 0.0361$. Females (B); ventrals: $y = 159.35 + 0.24x$; $n = 121$; $r = 0.1690$; $P = 0.0638$; $r^2 = 0.0286$; subcaudals: $y = 38.13 - 0.09x$; $n = 121$; $r = -0.1205$; $P = 0.1880$; $r^2 = 0.0145$. C: Temperature-related variations of number of ventrals/number of subcaudals ratio. Males: $y = 3.41 + 0.02x$; $n = 161$; $r = 0.2346$; $P = 0.0028$; $r^2 = 0.0550$; Females: $y = 4.12 + 0.02x$; $n = 121$; $r = 0.1953$; $P = 0.0318$; $r^2 = 0.0382$. ●: Males; △: Females.

1976; Madsen and Shine, 1993; Thorpe and Baez, 1993; Meiri, 2007). These variations in corporeal proportions, coloration or scalation patterns have several possible interpretations, and the factors influencing such morphological distinctions include the differences in survival and growth rates, as well as in nutrition, development and habitat conditions (Osgood, 1978; Schwaner and Sarre, 1988; Forsman, 1991; Arnold, 1993; Pearson *et al.*, 2002).

In *V. palaestinae* I noted several metric traits and ratios (SVL, M, and SVL/Lcap ratio) that enabled the separation of populations in the discriminant analyses. A geographically-dependent increase in corporeal proportions, assuming that the samples are more or less even-aged, can also be explained by the presence of latitudinal clines, which are often considered as a response to environmental (usually thermal) shifts (Bergmann, 1847; Ashton and Feldman, 2003). Ray (1960) and Lindsey (1966) showed that latitudinal clines in body dimensions, which are well noted for endotherms (Ashton *et al.*, 2000; Meiri and Dayan, 2003), may also apply to at least some ectotherms (Ashton and Feldman, 2003). Several studies support the position that some ectotherms follow Bergmann's rule (Atkinson and Sibly, 1997; Cruz *et al.*, 2005), whereas for other species the opposite pattern is true (Mousseau, 1997; Reed, 2003). Ashton and Feldman (2003), for example, found that turtles follow Bergmann's rule whereas lizards and snakes reverse it. In fact, within the observed geographical range of the present study, ambient temperature (annual mean) does not correlate with latitude; nevertheless, mean corporeal measurements in both sexes of the studied snake were high in the southern coastal plain. Hence, the present findings indicate that *V. palaestinae* does not obey Bergmann's rule or its converse. The recorded morphological trends would thus seem to reflect the influence of other factors, such as human pressure, diet, or local habitat conditions on the corporeal proportions of these vipers. It is interesting that a stable increase in body, head and tail linear size toward the south is more evident among females; males display a weaker size-latitude stability.

As shown above, in addition to geographic variance in linear head/body size, inter-sample differences were recorded for SVL/Lcap ratio. Such distinctions are often associated with concomitant feeding preferences (Arnold, 1993; Santos *et al.*, 2000), with morphological plasticity, as a response to dietary variation, is well documented among many snake species (Forsman and Lindell, 1991; Madsen and Shine, 1993). Prey size or shape is one of the

possible determinants of head and body size (Krause *et al.*, 2003). Several authors (Schwaner, 1985; Hasegawa and Moriguchi, 1989) have indicated that snakes are larger in areas where larger prey species occur. Well-documented and clearly distinguishable shifts in SVL were shown in an isolated population of tiger snakes (*Notechis scutatus*), reflecting the influence of diet, and the subsequent gradual process of genetic modification (Aubret and Shine, 2007). Earlier, Madsen and Shine (1993) suggested that body size geographic variability in grass snakes (*Natrix natrix*) is a result of phenotypic plasticity, reflecting an impact of prey availability, without any genetic changes having occurred within the populations. Forsman (1991) observed intraspecific variation in head length among *Vipera berus* populations, which are determined by the size of the consumed voles. Aubret *et al.* (2004) concluded that there are two reasons for the appearance of large heads in isolated populations of tiger snakes: the presence of genes that determine this and a facultative increase of head proportions as a consequence of large prey intake.

Vipera palaestinae is an opportunistic feeder (Volynchik, unpubl. data), whose diet mainly consists of rodents and small birds (including nestlings) and is determined by prey availability. My findings show that juvenile snakes living in or near farms and human settlements most often feed on house mice and young rats, while adult snakes feed on the large rats associated with human activity. In captivity, these vipers were shown to prefer gerbils (*Gerbillus*) among the possible rodent prey; rats were preferred to hamsters or voles; and spiny mice (*Acomys*) were the least acceptable (Mendelssohn, 1963). It is logical to assume that vipers that inhabit settlements and agricultural areas feed mostly on brown rats (*Rattus rattus*). This rat is very common and widespread in the Mediterranean region, and this abundant and relatively large rodent seems to be the easiest prey, providing the snakes with their long-term energy requirements. Among other small mammals, in natural habitats, adult *V. palaestinae* apparently consume the very common Mediterranean rodents, such as gerbils and jirds (*Gerbillus* and *Meriones*, respectively) and wood mice (*Apodemus mystacinus*, *A. sylvaticus*, *A. flavicollis*). Apparently, diet varies across the range depending on locality. Generally, in Israel, within most sites Palestine vipers are sympatric with Tristram's jirds (*Meriones tristrami*), which are abundant across most of the Mediterranean region (Mendelssohn and Yom-Tov, 1999) and grow to an average mass of 62–77 g. In the south, vipers also prey on *M. sacramenti*—an endemic rodent occurring along the

southern coastal plain. This species is the largest of all the gerbillids in Israel (Mendelssohn and Yom-Tov, 1999), attaining a weight of 175 g. The distribution of other possible prey, *Gerbillus pyramidum* and *G. andersoni*, partly overlap in the Tel-Aviv area, with the former being larger (average 101–108 mm; 35–40 g) and occurring on sandy soil of the southern coastal plain; whereas the latter (84–89 mm; 25–26 g; Mendelssohn and Yom-Tov, 1999) mainly inhabit the more vegetated biotopes of the central coastal plain. Hence, such size-latitude tendencies among the most common rodents across the observed samples' range, which is complicated also by the local abundance of brown rats (probably the largest prey for this snake > 200 mm and 200 g), has led to the appearance of inter-regional dietary distinctions. The divergences between localities and geographic groups presumably produced the specific morphological adaptations in corporeal dimensions and ratios to the consumption of large or small prey items.

Possible reasons for scalation variability have been frequently studied among many squamates. Thus, larger numbers of body scales (either MSR or ventral) are often explained by morphological adaptations to large body envelopment (Fabien *et al.*, 2004); in many snake species large-sized individuals have more ventral and dorsal scales (Klauber, 1956; Arnold, 1993; Lindell *et al.*, 1993; Shine, 2000). A high number of dorsal scale rows can also be explained by dietary divergence (Shine, 2002), while a higher MSR number provides greater stretch ability to the skin (Gans, 1974), which enables the consumption of large-sized prey items. Since *V. palaestinae* exhibits no significant correlation between SVL and number of ventral or dorsal (MSR) scales (Volynchik, 2011), the minor interpopulation variances in these features should be considered irrespective of body proportions.

In the present work I examined the impact of the thermal regime in their natural biotopes on the external morphology of adult specimens of this snake. I found a possible effect of temperature on body and tail scalation pattern that, primarily, may reflect the spatial variation in incubation temperature as affecting a specimen's phenotype. In Israel, in spite of its territorial compactness and relative spatial proximity between zoogeographic regions, along the distribution range of *V. palaestinae* we can observe a pronounced temperature gradient of averages and even more intense fluctuations of extreme values (see above), determined mostly by elevation. Average temperatures of the hottest month (August) range from 29.6°C at the bottom of depressions (–150–250 m below sea level), which are of course warmer than

the plains (26–27°C) or mountainous terrain, in which temperature rises to 24.5–25.5°C at the highest observed locations (800–900 m above sea level).

Reptiles, as ectotherms, are affected by exposure to a variety of abiotic environmental conditions, which during the gestation (incubation) period may induce a wide range of morphological variations (Deeming, 2004). Temperature-induced phenotypic changes have been detected among both oviparous (Shine *et al.*, 1997; Flatt *et al.*, 2001) and viviparous (Beuchat, 1988; Yan *et al.*, 2011) reptile species. The influence of thermal regime on gravid females can be buffered behaviorally (Shine, 1983; Peterson *et al.*, 1993), whereas post-oviposition the eggs are exposed to the ambient climatic conditions. Both experimental and field studies have demonstrated a profound impact of the thermal regime during embryonic development on offspring phenotype. This can manifest itself in many ways: e. g., variations in growth rate, body size, vertebrae number, scalation, and locomotor performance (Shine and Harlow, 1996; Shine *et al.*, 1997; Downes and Shine, 1999; Andrews and Mathies, 2000; Shine and Elphick, 2001; Webb *et al.*, 2001).

Temperature-related variation in vertebral number or ventral/subcaudal scale counts have been widely reported in many squamates (Klauber, 1941; Fox, 1948; Fox *et al.*, 1961; Werner, 1964; Ehrlich and Werner, 1993). Data reveal that the number of ventrals, reflecting vertebral numbers, is established during early embryogenesis (Hubert, 1985; Lindell, 1996), and remain constant throughout ontogenesis, in addition to frequently being heritable (Klauber, 1945; Arnold, 1988). Osgood (1978) noted that both low and high temperature conditions have an impact on scale count, degree of scalation variability, and the appearance of divided scales in *Natrix fasciata*. Among rattlesnake species occurring in both coastal and desert habitats, the latter tended to have, on average, more ventrals than the former (Klauber, 1941). Lourdaïs *et al.* (2004) demonstrated a significant impact of natural climatic conditions on ventral scalation in newborn aspik vipers; thus, hotter weather early on in gestation increases the number of ventral scales of neonates. Those authors also indicated a significant relationship between maternal and neonatal ventral scale counts in *Vipera aspis*.

The number of both ventral and subcaudal scales are two characters representing a particular functional interest and play a great role in snake systematics (Arnold and Bennett, 1988). In close functional interactions with other morphological components, such as muscles, vertebrae and ribs, these variables influence the individual fitness and survival of neonates (Gans, 1962; Lindell *et al.*,

1993). It is generally accepted that vertebrae number has been shown to correlate with the number of overlaying scales. A ratio of one vertebra to one ventral scale is the common condition in advanced snake taxa, including *Vipera* species (Kramer, 1961; Alexander and Gans, 1966). Indeed, a close correspondence between both body and tail scale counts and vertebral number was detected using x-ray in the garter snake *Thamnophis sirtalis* (Shine, 2000). However, it should be noted that some groups may differ from this ratio and have more ventrals per vertebra (Gans and Taub, 1965; Voris, 1975). Several studies have demonstrated a structural link between snout-vent length and the number of ventrals. For example, these two variables are correlated among some European vipers at both the specific and subspecific levels (Saint Girons, 1978; Nilson and Andr  n, 1986; Lindell *et al.*, 1993).

The present findings indicate that a thermal gradient across a natural habitat could significantly affect both body and tail scalation pattern in *V. palaestinae*. We might thus expect that these phenotypic trends (possibly reflected in body/tail vertebrae number differences) would be correlated by linear measurements, and the recorded opposite scalation changes result from corresponding body/tail ratio temperature-related shifts. However, testing the temperature-SVL/Lcd ratio relationship in both males and females did not confirm such a hypothesis. An increase in ventral scale number at hotter sites is not caused by lengthening of the body; and, vice versa, a decrease in subcaudal scale count does not reflect a “shrinking” of tails: mountain and valley specimens do not differ allometrically and possess a similar SVL/Lcd ratio. There are in fact no direct metric-meristic dependences, and the findings in this respect are consistent with an earlier study of *V. palaestinae* (Volynchik, 2011), which indicated no significant correlation between SVL and the number of ventrals; although a weak but significant (for a large sample size) correlation was observed between tail length and the number of subcaudals in both sexes.

In addition, the present findings demonstrate that environment does not influence the other scalation characters, including head pholidosis components (number of labial and circumorbital scales). One possible explanation for this is that either the ventral or subcaudal scales, due to a large variability at the intraspecific level (Volynchik, 2011), are easy target areas for the appearance of variations. The morphological data supporting this assumption are derived from a previous study on the same species, in which the temperature-correlated shifts in scale counts were more marked among males

displaying a greater variation of ventrals, and especially subcaudals, than in conspecific females (Volynchik, 2011). Concomitantly, head scales have very limited opportunities to exhibit variability in count and possible ecomorphological trends in these pholidosis features can only be detected within larger sample sizes. However, Fox (1948) observed the effect of prenatal temperatures on scale counts of newborn garter snakes: the offspring of females that had been kept under artificially decreased temperature had significantly fewer body (MSR, ventral) and tail scales, as well as fewer head (supralabial, postocular) scales.

In this study, the geographic regions differ in climate. It is thus logical to assume that such differences in temperature during pre- and especially post-oviposition periods (May-August for the first, August-October for the second; Mendelssohn, 1963) provide an opportunity for the appearance of scalation pattern variability at the intraspecific and interpopulation levels.

Since the present study was based on alcohol- and formalin-preserved specimens, their coloration might have changed or faded (Stuart, 1995; Simmons, 2002). I was thus unable to investigate color pattern changes across the distribution range. Mendelssohn (1963) did not find any relationships between pattern and distribution. However, Kochva (2004) reported that northern vipers (from the Golan Heights) are usually darker than more southern ones. In support of this I note that the darkest specimen was collected at the northernmost point of Israel (Mt. Hermon, 1250 m above sea level).

5. Conclusion

Vipera palaestinae in Israel seem to be generally quite homogeneous morphologically. At the same time, however, in natural habitats some external features of this species may also be influenced by the local environment, mainly ambient temperature. Despite the mean values of almost all morphological characters not significantly differing across the distribution range, linear measurements and ratios of both males and females showed a certain latitudinal variability that may reflect diet-induced phenotypic plasticity. However, a lack of available data on geographic variation in morphological traits and in diet composition of this viper from other parts of its range precludes the testing of these hypotheses. Several scalation characters contribute to the separation of geographic groups by multivariate comparison. Moreover, the number of ventral, subcaudal scales and their ratio (ventr/Scd) within both sexes noticeably correlates with

ambient temperature of the hottest month. The recorded temperature-induced scalation variability does not reflect a significant body length-ventral scales and tail length-subcaudal scales correlation. The marked variances in scale counts would seem to reflect the temperature gradient across the geographic range of this species, which affects scale development during embryogenesis, and thus may indicate the potential evolutionary importance of environmental conditions.

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